

STRUCTURE AND TAXONOMY OF TAENIOMA, INCLUDING A DISCUSSION ON THE PHYLOGENY OF THE CERAMIALES

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The genus *Taenioma* was founded by J. Agardh (2) in 1863 to receive a species which he (1) had previously described as *Poly-siphonia perpusilla*. He placed *Taenioma* in the Rhodomelaceae while Schmitz (41) in 1889 included it in his newly created Sarcomenieae, a sub-family of the Delesseriaceae. In conjunction with his monograph on the Rhodomelaceae, Falkenberg (14) also studied *Taenioma* with the specific purpose of demonstrating, by way of contrast, the differences in construction of the thallus between the Rhodomelaceae and Delesseriaceae. The majority of later writers (De Toni, 12, 13; Børghesen, 5, 6; Kylin, 28; and others) who have been concerned with this genus have followed Schmitz and Falkenberg in assigning it to the Delesseriaceae.

Subsequent to the work of Falkenberg, the most important paper on *Taenioma* has been that of Thompson (43) in 1910. Thompson discovered cystocarps for the first time in the genus and from a somewhat superficial study of them concluded that *Taenioma* belonged in the Rhodomelaceae. Recently this view was also adopted by Hollenberg (19). Thompson and Hollenberg, however, overlooked the most significant structural feature distinguishing the Delesseriaceae from the Rhodomelaceae, namely, the difference in the order of formation of the pericentral cells. As was shown by Falkenberg, the pericentral cells in *Taenioma* are formed in the manner characteristic of the Delesseriaceae. This question will be taken up more fully in later pages, after the structure of the thallus has been reviewed.

Kylin (24) in 1923 pointed out that the Sarcomenieae should be united with the Delesseriaceae, a conclusion borne out by the work of Papenfuss (35) on *Claudea* and *Vanvoorstia*. Knowledge concerning the structure and reproduction of the majority of other genera in this old sub-family is meager. Through the work of Falkenberg (14), Thompson (43), Thuret (9), Børghesen (5) and Okamura (33), *Taenioma* has become one of the better-known members of the Sarcomenieae. Although sexual organs were not present in the writer's material, certain observations on the structure of the thallus and the development of the tetrasporangia seem worthy of record.

The anatomical work in the present study was made on Hawaiian and South African plants of *Taenioma perpusillum*. The South African material was kindly supplied by Dr. Mary A. Pocock who collected it at Arniston (May 7, 1940) and Port Elizabeth (Dec. 8, 1942, with tetrasporangia). The species has been

reported as occurring in South Africa. The record is based on Kützing's (23) *Polysiphonia nana*; but, as will be pointed out farther on, it is very doubtful if *P. nana* is representative of *Taenioma*. The Hawaiian material was collected by the writer during the years 1940-42 at the following localities on the island of Oahu: Hanauma Bay (March 30, 1941); 1.8 miles northwest of Nanakuli (May 16, 1942, with tetrasporangia); Waikiki (Nov. 17, 1940, and Aug. 21, 1941). Additional Hawaiian material was kindly furnished by Mrs. D. Abbott who obtained it on the ascidian *Pyura momas*, collected by members of the Department of Zoology of the University of Hawaii, at Kaneohe Bay, Oahu (Feb. 11, 1941, with tetrasporangia). All the material collected by the writer was obtained in the intertidal zone, where the species occurs as an epiphyte on *Bornetella* and a variety of small turf-forming algae. *T. perpusillum* had been reported from Hawaii in 1880 by Chamberlain (10) but the record has escaped notice.

The Hawaiian and South African plants seem to be identical in every respect. South African specimens received from Dr. Pocock in 1939, while the writer was working at Lund, were compared with the type material of *T. perpusillum* (nos. 43342 and 43343 in Herb. Agardh) and found to correspond very well. Since only dried South African plants were available for the present study, the following account is based entirely upon observations on Hawaiian material, which was preserved in formalin.

STRUCTURE OF THALUS

Taenioma is a small alga, measuring less than three millimeters in height, and consisting of a prostrate, terete, branched, indeterminate main axis, attached by non-septate rhizoids on the ventral side and forming erect, terete, secondary indeterminate axes on the dorsal side. According to Falkenberg (14), the erect branches are determinate, but from the writer's observations there seems to be no evidence for this. Both prostrate and erect axes are monopodial and grow by means of a single transversely-dividing initial. The axes are composed of segments consisting of a central and four pericentral cells. The rhizoids arise as outgrowths from the ventral pericentral cells of the prostrate parts. The ascending axes are formed alternately at an interspace of three to eight segments, and by bending upward give the impres-

EXPLANATION OF THE FIGURES. PLATE 23.

PLATE 23. *TAENIOMA PERPUSILLUM*. FIG. 1. Portion of thallus showing an erect axis with alternate determinate branches and with indeterminate branches on the adaxial side of the latter, $\times 125$. FIG. 2. Portion of a determinate branch with three young apical hairs, $\times 600$. FIG. 3. Distal ends of determinate branches showing the terminal monosiphonous hairs, $\times 125$. FIG. 4. Basal region of a determinate branch with mature tetrasporangia, $\times 600$.

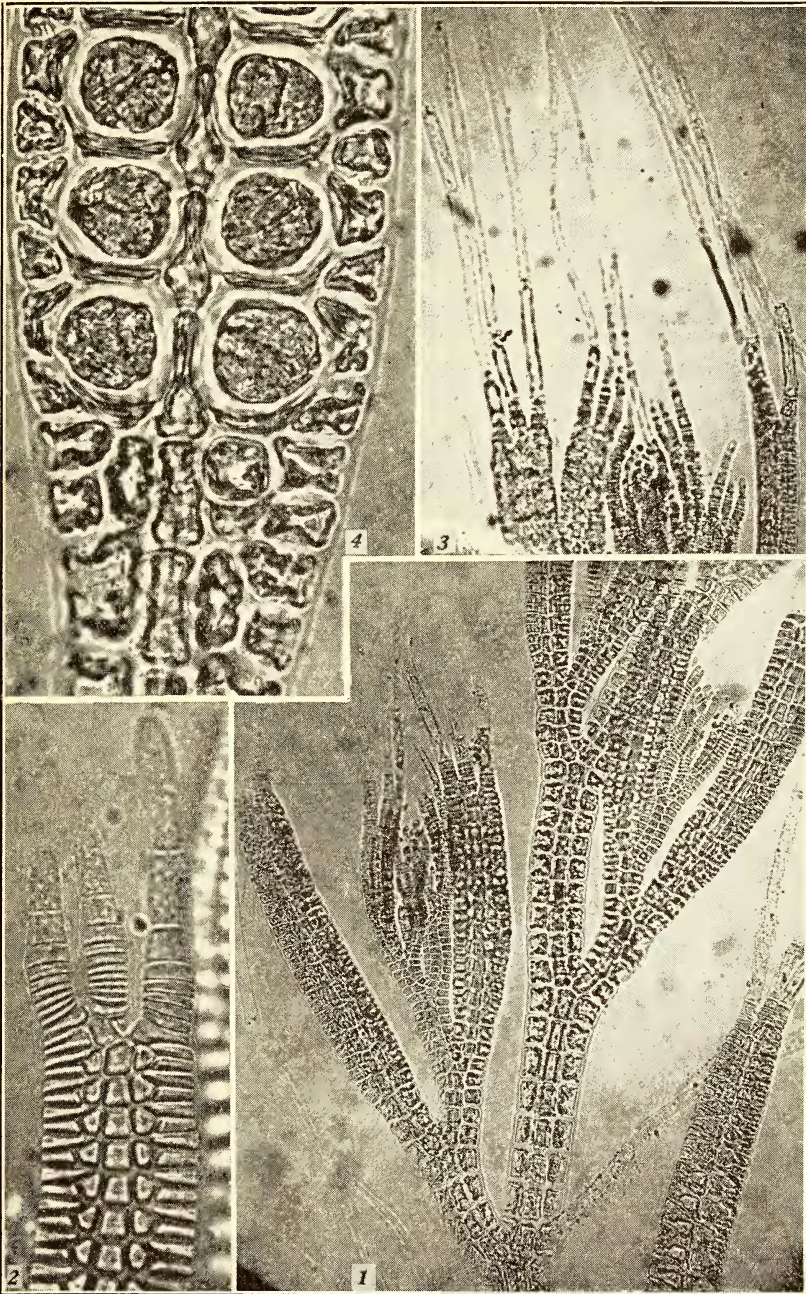


PLATE 23. TAENIOMA PERPUSILLUM. Photomicrographs by T. T. McCabe.

sion of having arisen in a second series from the dorsal side of the prostrate axis.

Starting at the third, fourth or fifth segment from the base, the erect secondary axes give rise to determinate branches alternately at an interspace of two to nine segments (fig. 1). These branches, in contrast to the indeterminate axes, are five cells in width, except at the base, and are therefore flat (figs. 1, 2, 11, 12, 14). At an early stage in development, three hairs are formed at the tip of each determinate branch (figs. 1-3, 11-14) whereupon all further growth in length by segment formation ceases in such a branch.

When a developing determinate branch is two or three segments long, it frequently initiates on its adaxial side an indeterminate branch which in a manner similar to the secondary axes forms determinate branches of a higher order (figs. 1, 7; see also Thompson, 43, fig. 3). This process whereby a determinate or an indeterminate branch of one order gives rise to a higher order of branch of the opposite type is repeated over and over.

METHOD OF BRANCHING. When a branch is to be initiated, the apical cell, which ordinarily divides transversely, forming disk-shaped segments, divides by an oblique wall, leaving a segment which on one side is higher than the other (figs. 5, 7). Through enlargement the higher side of this segment forms a protuberance which is cut off. The cell so formed is the initial of a branch (fig. 6). This method of branching has been termed exogenous branching by Falkenberg (14). The original initial retains its rôle as the apical cell of the axis. Both apical cells next divide in the usual transverse fashion, giving rise to two monosiphonous filaments whose segments eventually undergo division. In the case of the erect axes, the branches formed are always alternate and of the determinate type while the prostrate main axis forms alternate and commonly erect, indeterminate branches. As stated above, a determinate branch usually forms an indeterminate branch on its adaxial side (figs. 1, 7). These branches are also exogenous in origin.

Although indicated in Falkenberg's (14) figure 23 on plate 15, and described and figured by Thompson (43, p. 100, fig. 4), the exogenous manner of branching in *Taenioma* has not received recognition commensurate to its importance. This method of branching is of common occurrence in the Rhodomelaceae, Dasycaceae, and Ceramiaceae but is rarely met with in the Delesseriaceae. In other members of this family, the branches are formed in one or more of the following ways: (1) marginal as in *Membranoptera alata* (Kylin, 24, p. 110, fig. 70), (2) from a cortical cell on the midrib as in *Apoglossum ruscifolium* (Kylin, 24, pp. 85-86, fig. 55b), (3) endogenously as in *Claudea* and *Vanvoorstia* (Papenfuss, 35), or (4) entirely adventitiously from cortical cells

as in *Membranoptera alata* (Phillips, 37) and *Claudea multifida* (Papenfuss, 35).

The only other member of the Delesseriaceae which is known to show exogenous branching is *Caloglossa*. Nägeli (32) as long ago as 1855 showed that in *C. Leprieurii* the branches are initiated by segments which are formed as the result of an oblique division of the apical cell of the parent branch (Nägeli, *op. cit.*, p. 71, pl. 8, figs. 9-10). He also pointed out that the axis is monopodial and that the branches are alternate in position. In manner of growth and branching *Caloglossa* thus agrees with *Taenioma*. It should be mentioned, however, that in *Caloglossa* branches also occur on the midrib, but the exact method of their initiation is unknown. In general, Nägeli's work has not been correctly interpreted, since it is usually stated that in *Caloglossa* the lateral branches are marginal in origin.

STRUCTURE OF DETERMINATE BRANCHES. The determinate branches are formed alternately at an interspace of two to nine segments on the terete, erect, indeterminate branches (fig. 1). The apical cell of the young branch by transverse division forms segments in the manner characteristic of the Delesseriaceae. When a determinate branch is but two or three segments long, its apical cell frequently divides by an oblique wall, cutting off a segment which gives rise to an indeterminate branch on the adaxial side (fig. 7). Following the initiation of this branch, the apical cell by transverse divisions forms from 12 to 20 segments. There are then formed by alternate oblique divisions two segments (fig. 8) which are similar to those which initiate branches. Each of these two segments gives rise to an apical cell (figs. 9, 10). At this stage, the branch apex is thus crowned with three initials. The latter by transverse division give rise to the three monosiphonous hairs which adorn the tip of the mature determinate branch (figs. 10-14, 2-3).

As has been pointed out by Falkenberg (14) and Thompson (43), the hairs terminate all growth in length by cell formation and are responsible for the determinate character of these branches. According to Børgesen (5) and Okamura (33), intercalary divisions occur at the base of a hair, but the writer can find no evidence of this. The cells of the hairs are formed in acropetal succession by division of the apical cell. Those at the base merely fail to elongate as much as the distal ones and give the false impression of having been formed by intercalary divisions.

While the hairs are in course of formation, the part of the determinate branch posterior to them continues its development. This is best described in connection with figures eight and eleven to thirteen.

At the time that the hairs are initiated, the segments immediately below the two hair-forming ones are still undivided (fig. 8).

The division of the segments to form pericentral cells is shown in figure eleven. It will be seen from this figure that the second and third segments below the large triangular cell, representing the segment which initiated the first hair, have each formed a lateral pericentral cell, while in the following three segments both lateral pericentral cells have been formed. In the seventh and subsequent segments down from the triangular cell, both the transverse pericentral cells have been cut off, but only one in each segment is indicated in the figure. At this stage the segments thus consist of a central and four pericentral cells.

Mature determinate branches, in contrast to indeterminate ones, are flat, except for the segments below and the three to five immediately above the place of insertion of the daughter indeterminate branch, which remain cylindrical. This flat form is produced as the result of the formation of two flanking cells by each of the lateral pericentral cells.

The transverse pericentral cells do not divide and the branch consequently remains only three cells in thickness at the midrib. The method of formation of the flanking cells is shown in the lower three segments in figure twelve. It will be seen that the pericentral cells first divide by an oblique wall, more or less transverse to the branch axis, to form a flanking cell toward the branch apex. The next division is also in a vertical plane and cuts off the second flanking cell from the portion of the pericentral cell below the first-formed flanking cell. After the four flanking cells have been cut off, no further divisions occur in the segments of a determinate branch.

EXPLANATION OF THE FIGURES. PLATE 24.

PLATE 24. TAENIOMA. FIGS. 5-16, *Taenioma perpusillum*. FIG. 5. Oblique division of the apical cell of an indeterminate branch to form a branch-initiating segment. FIG. 6. Division of a branch-initiating segment to form an apical cell, the cell to the right. FIG. 7. An indeterminate axis with two alternate young determinate branches, each of which has initiated an adaxial indeterminate branch, while the apical cell of the axis has divided by an oblique wall in preparation for the formation of a determinate branch to the right (the oldest of the determinate branches, the one to the right, is in an early stage of hair-formation, as seen in a side view of its apex). FIGS. 8-10. Early stages in the formation of the three terminal hairs, the central initial representing the original apical cell of the branch. FIGS. 11-13. Young determinate branches showing the further development of the hairs and the division of the segments of a branch initial to form a central cell, four pericentral cells, and the two cells which flank each of the lateral pericentral cells. FIG. 14. Optical longitudinal section parallel to the surface of a determinate branch showing early stages in the formation of tetrasporangia (cover cells were present in the two lower segments but are not indicated in the figure). FIG. 15. Optical vertical section through a row of fertile lateral pericentral cells of a tetrasporangia-bearing branch showing the formation of two cover cells by the stalk cell in the two older segments. FIG. 16. Optical longitudinal section parallel to the surface of a determinate branch with mature tetrasporangia. FIG. 17. *Taenioma macrourum*, terminal portion of a young determinate branch with its two apical hairs in the course of development (material from the Bahamas, *Howe 5708*). (Figs. 5-15, 17, $\times 780$. Fig. 16, $\times 340$.)

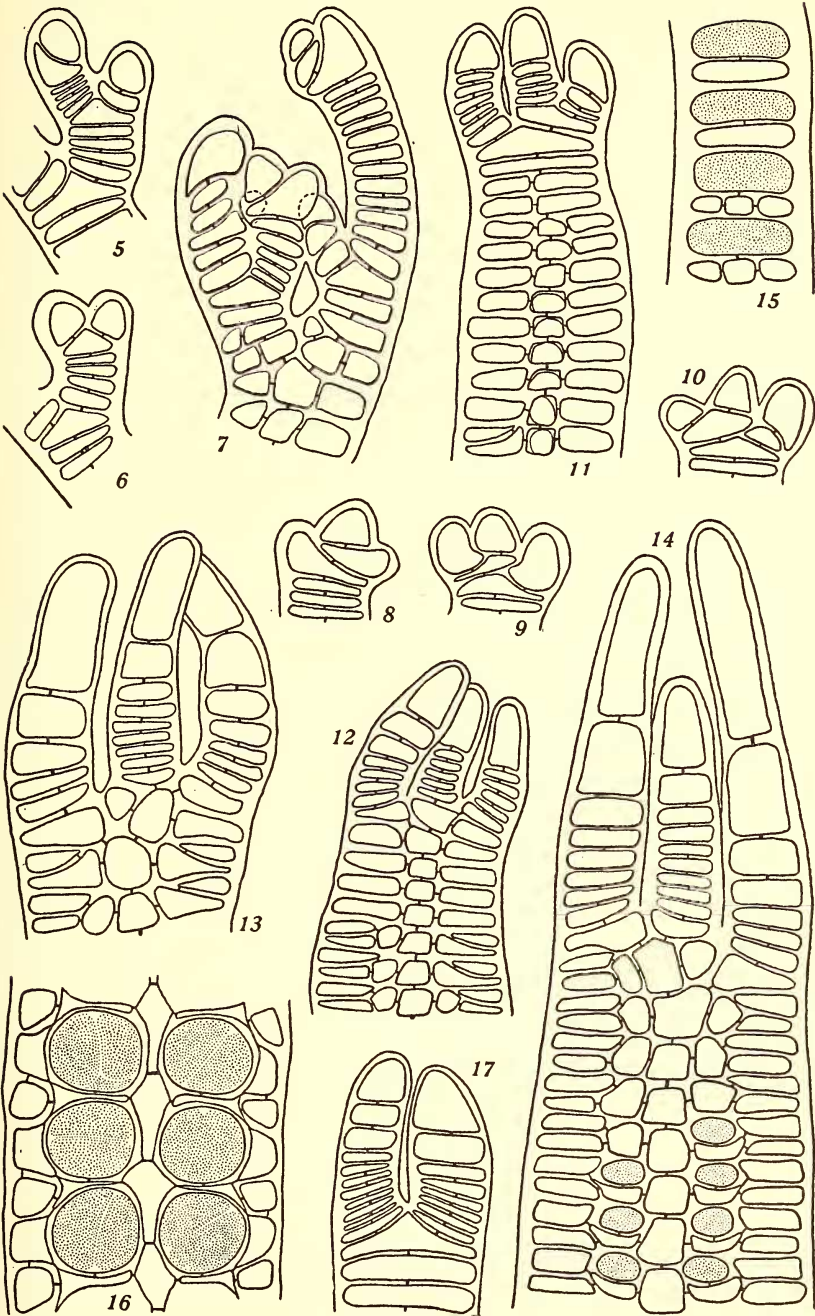


PLATE 24. TAENIOMA.

The division of the two hair-forming segments is similar to that of other segments (figs. 12-14), except that in the distal one, the lateral pericentral cell on the side opposite to the point of attachment of the hair fails to form flanking cells (figs. 2, 14).

No intercalary cell divisions occur anywhere in the thallus of *Taenioma*. Secondary pit connections are formed between neighboring cells, except in the case of the central cells, which do not become secondarily connected to each other nor to other cells.

Although the thallus of *Taenioma* is extremely simple, the construction of the determinate branches is nevertheless in accordance with the plan basic to all Delesseriaceae (cf. Kylin, 24, pp. 67-69, 81-82). Three categories of cells may thus be recognized: (1) a cell-row of the first order, represented by the central cells; (2) a cell-row of the second order, represented by the lateral pericentral cells and the upper of the two flanking cells; and (3) a cell-row of the third order, represented in the determinate branches of *Taenioma* by a single cell, the lower of the two-flanking cells (figs. 2, 12-14).

It was stated earlier that *Taenioma* is to be included in the Delesseriaceae rather than in the Rhodomelaceae on the basis of the sequence in which the pericentral cells are formed.

That there is a fundamental difference in the order of formation of the pericentral cells in the Rhodomelaceae and Delesseriaceae was first pointed out by Nägeli (31) in 1847. From his studies of *Hypoglossum Woodwardii*, species of *Polysiphonia* and other representatives of both Delesseriaceae and Rhodomelaceae, Nägeli (29, 30, 31) established that in the Delesseriaceae the two lateral pericentral cells are formed before the two transverse ones (Nägeli, 29, pl. 1, fig. 9). In the Rhodomelaceae, on the other hand, the pericentral cells are formed in a progressive alternate sequence, with reference to the first one, until the circle is completed. The last-formed pericentral cell thus occupies a position diametrically opposite the first-formed (Nägeli, 30, pl. 7, figs. 33-37).

Since the time of Nägeli, hundreds of species of both Delesseriaceae and Rhodomelaceae have been studied by a large number of workers but not a single exception to these plans has been found. In the manner typical of the Delesseriaceae, the two lateral pericentral cells are also the first to be found in *Taenioma* (fig. 11; see also Falkenberg, 14, p. 710, pl. 15, figs. 25-26; and Thompson, 43, p. 101).

In the Delesseriaceae, with the exception of *Taenioma* and *Caloglossa*, lateral organs are not initiated by a segment prior to the formation of its pericentral cells. In the majority of Rhodomelaceae, to the contrary, the lateral organs are initiated before the segment cells have formed pericentral cells. Subsequent to Nägeli, many workers have consequently been concerned with problems relating to the position of the pericentral cells

with reference to the lateral organs and to one another. The following are some of the more important questions which have been studied: (1) the position of the first pericentral cell, (2) whether the second pericentral cell is formed to the left or to the right of the first, (3) whether or not the position of the second pericentral cell is constant in a given species, and (4) whether or not the second pericentral cell follows the spiral described by the lateral organs. For a summary of knowledge concerning these interesting questions, the reader is referred to the excellent paper by Rosenberg (38, pp. 5-9, 31-32).

In this connection, it may be mentioned that in the Dasyaceae, according to Rosenberg (38), the pericentral cells are formed in a progressive left-hand sequence, with reference to the first one, as seen from the outside, so that in the completed circle the youngest lies to the right and next to the first-formed. The Dasyaceae, Delesseriaceae and Rhodomelaceae thus differ very sharply from one another in regard to the plan in which the pericentral cells are formed. In the remaining family of the Ceramiales, the Ceramiaceae, typical pericentral cells are of course not formed.

In addition to the difference in plan of pericentral cell formation, the Delesseriaceae may also be distinguished from the Rhodomelaceae, as was pointed out by Falkenberg (14, p. 713), by the fact that in the Delesseriaceae the lateral pericentral cells always form two flanking cells, which in the majority of forms function as the mother-cells of initials which give rise to lateral rows of cells. Each of these flanking cells has a primary pit-connection with the pericentral cell and their combined length equals that of the pericentral cell.

In the few examples of Rhodomelaceae where a similar formation of flanking cells occurs, only one flanking cell is formed by each pericentral cell. This cell is cut off by a longitudinal division and is therefore as long as the pericentral cell. It may later divide transversely so that there are two (or more ?) flanking cells. Only one of these cells, however, will be united to the parent pericentral cell by a primary cytoplasmic connection.

In regard to the manner of flanking cell formation *Taenioma* thus also shows itself to be a member of the Delesseriaceae.

REPRODUCTION

TETRASPORANGIA. Several of the earlier workers have recorded tetrasporangia in *Taenioma*. The development of these organs has, however, been studied only by Thompson (43). The writer's observations are in agreement with those of this author.

The sporangia are cut off in acropetal succession from the lateral pericentral cells in the expanded distal portion of the determinate branches (fig. 14). Each pericentral cell forms only one sporangium. It is separated by a concave wall from the

terminal end of the pericentral cell and is in cytoplasmic communication with this cell only (fig. 14).

After a sporangium has been initiated, the remaining portion of the pericentral cell, at this stage referred to as the stalk cell, divides by two walls parallel to the surfaces, forming a small cover cell on each (fig. 15). In *Taenioma* the cells so formed never enlarge or divide to form a protective layer over the sporangium, but remain as rudimentary cover cells on either surface of the stalk cell. The sporangia thus remain exposed on two sides during their entire existence (figs. 4, 16). In the mature sporangia-bearing branch, the central cells of the branch and the stalk cells of the sporangia are considerably stretched by the enlarging sporangia, and the marginal cells become connected by secondary pit-connections to neighboring marginal and stalk cells (fig. 16).

The method of sporangium-formation in *Taenioma* is comparable to that in *Vanvoorstia* (Papenfuss, 35, figs. 67, 68). In both genera the sporangia are formed by pericentral cells which have not yet become corticated, and the cover cells are formed after the sporangia have been initiated. The subsequent development in the two genera is different, however, in that the primary cover cells grow and divide in *Vanvoorstia*, forming a complete protective tissue over the sporangia, whereas in *Taenioma* the cover cells serve no protective purpose and the sporangia remain exposed.

By the method of sporangium-formation, *Taenioma* thus again shows itself to be a member of the Delesseriaceae. In the Rhodomelaceae, the pericentral cells destined to produce sporangia first form two cover cells by longitudinal divisions and then divide by a transverse wall to form the sporangium (cf. Kylin, 28, p. 173). The situation in the Rhodomelaceae is thus the reverse from that in *Taenioma* and *Vanvoorstia* where the sporangium is the first cell to be cut off by a fertile pericentral cell.

In those Delesserieae and Rhodomelaceae in which the sporangia are initiated by cells other than the pericentral cells this sequence is maintained (cf. Kylin, 28, pp. 170, 174-175). The significance of this distinction between the Delesserieae and Rhodomelaceae will appear later.

SPERMATANGIA AND CYSTOCARPS. Sexual organs have been but rarely observed in *Taenioma*. None were present in the writer's material. Spermatangia were recorded for the first time by Schmitz and Hauptfleisch (42, p. 415) in 1897, and for a second time by Thompson (43) in 1910. From the descriptions of these authors and from the figures of Thompson, it is clear that the spermatangia are formed directly on the branches (the determinate branches) as they are in all other Delesseriaceae. In the Rhodomelaceae the spermatangia are usually formed on trichoblasts, although, as pointed out by Falkenberg (14), there are exceptions to this rule. In a few genera such as *Bostrychia* and

Rhodomela, the spermatangia are formed on ordinary polysiphonous branches.

According to Thompson, the lateral pericentral cells become divided by vertical walls prior to the formation of spermatangial mother-cells. This statement requires verification. In other monostromatic Delesseriaceae the primary cells become divided by two walls parallel to the surface, forming a layer of cells on each surface. The superficial cells so formed then become divided by vertical walls to form the spermatangial mother cells. The spermatangia are formed on the surface of these cells. The mature spermatangial sorus is thus composed of five cells in thickness. Thompson describes and figures the mature sorus of *Taenioma* as consisting of four cells in thickness.

Cystocarps have been observed with certainty only by Thompson (43). The record by Collins and Hervey (11) of a mature cystocarp in material from Bermuda (Phyc. Bor.-Amer. no. 1935) is very doubtful, since duplicate material of this collection which was examined by Howe (20) proved to be a rhodomelaceous alga. The writer has found the same to be true of the duplicate material in the Herbarium of the University of California.

Nothing is known of the development of the procarp in *Taenioma* and very little concerning the cystocarp. According to Thompson, the cystocarps occur on the terete branches. This may seem unusual in view of the fact that the sporangia and spermatangia occur on the flattened determinate branches. From the position of the cystocarp Thompson concluded that this organ is a modified branch. This assumption is logical. It seems likely, however, that the cystocarps are initiated on young determinate branches but that such branches do not complete their normal growth and in the course of development of the cystocarp become incorporated in its wall. Comparable conditions obtain in *Claudea* and in *Vanvoorstia* (cf. Papenfuss, 35, pp. 26, 43, figs. 23, 42, 43, 51).

From the general shape of the cystocarp and the gross structure of the gonimoblast, Thompson concluded that *Taenioma* belonged in the Rhodomelaceae. Through the researches of Falkenberg and of Kylin and his students, we now know, however, that there are no sharply defined and constant differences between the Rhodomelaceae and Delesseriaceae with respect to the development and structure of the cystocarp.

TAXONOMY

In addition to *T. perpusillum*, which was described by J. Agardh (1, 2) from material collected by Liebmann at St. Augustin on the Pacific coast of Mexico, two other species, *T. macroum* Thuret (9) and *T. Clevelandii* Farlow (15), have been credited to *Taenioma*.

Taenioma macrourum was established by Thuret in 1876 upon material collected by Schousbee at Tangier, Morocco. In considering his plant as distinct from *T. perpusillum*, Thuret seems to have been influenced more by the widely separated stations of the two species than by morphological differences. Without being aware of it, he did, however, describe and figure a feature whereby *T. macrourum* can readily be distinguished from *T. perpusillum* as characterized by J. Agardh. According to Thuret the tetrasporangia-bearing branches of *T. macrourum* terminate in two hairs while those of *T. perpusillum*, according to J. Agardh, end in three hairs. This character is of the first importance in separating these two species as will be shown farther on.

Bornet (8) in 1892 reduced *T. macrourum* to the synonymy of *T. perpusillum*, and this point of view has been accepted by the majority of workers, including De Toni (12), Howe (in Thompson, 43, p. 98, note), Børgesen (5, 6), Okamura (33) and others. Falkenberg (14) and Schiffner (39, 40), on the other hand, have retained *T. macrourum* as an independent species. Schiffner does not give his reasons for so doing but Falkenberg, upon comparing *T. perpusillum* from the Pacific with material of *T. macrourum* from the Mediterranean, concluded that the former species lacked the long monosiphonous terminal hairs characteristic of the latter. The branches in *T. perpusillum* were also separated by an interspace of more segments, causing the plants to be less compact than in *T. macrourum*.

Although it is not possible to uphold the characters relied upon by Falkenberg, the writer's study nevertheless favors separation of the two species. As mentioned earlier the plants at hand of *T. perpusillum* came from Hawaii and South Africa. The observations on *T. macrourum* are based upon material from the Bahamas (*Howe 5708*, as *T. perpusillum*—Herb. Univ. Calif. no. 207218) and from the Adriatic (Schiffner, Alg. mar. no. 860—Herb. Univ. Calif. no. 495029).

From the account of the structure of the determinate branches of *T. perpusillum* it is seen that the terminal hairs are formed in a very precise manner. In this species the apical cell of a developing determinate branch forms a number of disk-shaped segments by transverse divisions and then, by alternate oblique divisions, two segments which on one side are higher than the other. These two segments form initials which together with the original apical cell of the branch give rise to the three terminal hairs characteristic of this species. In *T. macrourum* only one terminal segment is formed by an oblique division of the apical cell of a determinate branch and as a result the tips of these branches are crowned with only two hairs (fig. 17; also see Thuret, 9, pl. 25, fig. 1; Falkenberg, 14, pl. 15, figs. 21, 22; Børgesen, 5, fig. 337).

Since none of the plants studied by the writer showed part of the branches ending in three hairs and the rest in two, there

is reason to believe that the number of hairs is constant in a species: in *T. perpusillum* the determinate branches invariably end in three hairs while in *T. macrourum* they end in two.

Another feature which may be of importance in separating *T. perpusillum* from *T. macrourum* is that in the former the determinate branches usually form an adaxial indeterminate branch near their base, while in the latter such branches are rare. Consequently in *T. perpusillum* the thallus is more profusely branched than in *T. macrourum*. Before it could be conclusively stated, however, that this latter character is of systematic value, it would be necessary to examine more material of *T. macrourum* than has been available to the writer.

Bornet (8) when uniting *T. perpusillum* and *T. macrourum* listed as a synonym the South African species described by Kützing (23) in 1863 as *Polysiphonia nana*, while Falkenberg (14) gave the latter as a synonym of *T. macrourum*. Kützing figured *P. nana* as having some branches ending in a large inflated, apical cell and others ending in two hairs. If *P. nana* were a species of *Taenioma*, it would thus be logical to consider it as representative of *T. macrourum*; and since *nana* is the older specific name it would have priority over *macrourum*. The writer has not had the opportunity of examining Kützing's material nor has he been able to identify with certainty a South African plant with Kützing's species. Judging from Kützing's description and figure, however, there is little reason for believing that *Polysiphonia nana* is representative of the genus *Taenioma*. It seems more likely that the species is a rhodomelaceous alga. The segments show four parallel, vertically elongated, cells of the same length, which suggest pericentral cells as seen in surface view.

The third species of *Taenioma*, *T. Clevelandii*, was described by Farlow (15) in 1877 from material collected by Cleveland at San Diego, California. In a recent paper Hollenberg (19) records having again found the species; and he also refers to specimens in the Herbarium of the University of California. According to Hollenberg *T. Clevelandii* was reduced to the synonymy of *T. perpusillum* by De Toni (13). The cited work of De Toni, however, contains no statement to this effect.

From a study of the material in the Herbarium of the University of California and from the account of Hollenberg, it is clear that *T. Clevelandii* is not a species of *Taenioma* but belongs to the genus *Platysiphonia* Børgesen (7). Weber-van Bosse (45) already in 1896 remarked upon the great similarity in structure between *T. Clevelandii* and *Sarcomenia miniata*, which is now *Platysiphonia miniata*. *T. Clevelandii* differs from the other two species of *Taenioma* in the following important features which it shares with *Platysiphonia*: (1) The branches are endogenous in origin. (2) No terete branches are formed, that is, the lateral pericentral cells in all branches divide to form two flanking cells. (3) It does not

have determinate branches which end in hairs. (4) In the tetrasporangia-bearing branches, the sporangia on one surface are covered by a large cell and on the other by a rudimentary cover cell. These branches thus have a dorsiventral organization. In *Taenioma* both cover cells are rudimentary.

In habit *T. Clevelandii* resembles *Platysiphonia intermedia*. The relation of these species to each other can, however, only be established from a detailed comparative study based on preserved material. Pending such a study, it seems best to retain them as distinct entities.

The nomenclature and the geographical distribution of the species of *Taenioma* may be summarized as follows:

TAENIOMA PERPUSILLUM (J. Ag.) J. Agardh, Sp. Alg. 2(3): 1257. 1863. *Polysiphonia perpusilla* J. Agardh, Öfvers. Kgl. Svenska Vetensk.-Akad. Förhandl. 4: 16. 1848.

Geographical distribution. PACIFIC OCEAN: St. Augustin, west coast of Mexico (type locality, J. Agardh, *loc. cit.*); Hawaiian Islands (Chamberlain, 10, p. 33; Papenfuss in the present article); Japan (Okamura, 33, p. 26, in part); Tonga Islands (Grunow, 17, p. 50); Molucca Islands (Heydrich, 18, p. 295). INDIAN OCEAN: Dirk Hartog Island, Western Australia (Askenasy, 3, p. 54); South Africa (Papenfuss in the present article). ATLANTIC OCEAN: Puerto Rico (Thompson, 43, p. 97).

TAENIOMA MACROURUM Thuret, in Bornet and Thuret, Notes Algologiques, Fasc. 1: 69. 1876.

Geographical distribution. MEDITERRANEAN SEA: Tangier, Morocco (type locality, Thuret, *loc. cit.*; Bornet, 8, p. 297, as *T. perpusillum*); Balearic Islands (probably this species, De Toni, 13, p. 358, as *T. perpusillum*); Naples (Berthold, 4, p. 523; Falkenberg, 14, p. 709); Dalmatia, Adriatic (Schiffner, 39, p. 158—Alg. mar. no. 860!; 40, p. 302). ATLANTIC OCEAN: Canary Islands (Børgesen, 6, p. 143, as *T. perpusillum*). CARIBBEAN: Caracas, Venezuela (Bornet, 8, p. 297, as *T. perpusillum*), Barbados (probably this species, Vickers, 44, p. 62, as *T. perpusillum*), Bahamas (Thompson, 43, p. 97; Howe, 21, p. 564, as *T. perpusillum*, *Howe 5708*!), Virgin Islands (Børgesen, 5, p. 338, as *T. perpusillum*). PACIFIC OCEAN: Japan (Okamura, 33, p. 26, as *T. perpusillum*, in part).

Platysiphonia Clevelandii (Farlow) Papenfuss, comb. nov. *Taenioma Clevelandii* Farlow, Proc. Am. Acad. Arts and Sci. 12: 236. 1877.

Geographical distribution. CALIFORNIA: San Diego (type locality, Farlow, *loc. cit.*); San Pedro (Herb. Univ. Calif. no. 96445, Mrs. H. D. Johnston, Jan. 27, 1900, with tetrasporangia; no. 315651, H. P. Johnson, Dec. 28, 1895); Carmel Bay (Herb.

Univ. Calif. no. 274026, *N. L. Gardner*, May, 1916, with tetrasporangia); near Pacific Grove (Hollenberg, 19, p. 534).

DISCUSSION

From the preceding account of the structure of the thallus and the development of the tetrasporangia it is clear that Falkenberg (14) was justified in removing *Taenioma* from the Rhodomelaceae and placing it in the Delesseriaceae. Within this family the genus belongs in the sub-family Delesserieae; and from a comparison with other genera, it is apparent that *Taenioma* is the simplest of known Delesserieae. This is shown both by the structure of the thallus and the exposed condition of the sporangia. In the indeterminate branches, the lateral pericentral cells do not function as the mother-cells of lateral initials, while in the determinate branches, where they do act as such, the cell-row of the second order is composed of but two cells and that of the third order is represented by only one cell. As in other Delesserieae, the sporangial mother-cells first form a sporangium and later the cover cells; but in contrast to other members of this sub-family the cover cells in *Taenioma* are of a rudimentary character and at best can only be classed as incipient cover cells. They have no protective value at any stage in the development of the sporangia. These organs consequently always remain exposed on two sides.

In his monograph on the Delesseriaceae, Kylin (25) divided the family into a number of groups. To these was added the *Claudea*-group by Papenfuss (35). *Taenioma* possesses certain of the characters of the latter group but differs from it and all other groups in one very important feature, namely, the exogenous origin of the branches. This method of branch initiation is, however, also shown by *Caloglossa*, which Papenfuss included in the *Claudea*-group. *Caloglossa* was placed in this group on the basis of the structure of the blade and the formation of procarps on only one surface of the blades; and since it has generally been supposed that the branches in *Caloglossa* are marginal in origin, the *Claudea*-group was circumscribed so as to include forms with this method of branching. From the work of Nägeli (32) it is obvious, however, that the branches in *Caloglossa* are exogenous in origin. It thus becomes necessary to remove this genus from the *Claudea*-group, and to amend the group so as to exclude forms showing marginal branching.

Since *Taenioma* and *Caloglossa* differ from all other known Delesseriaceae by the exogenous origin of their branches, it seems likely that these genera will prove to be closely related. This question could be considered more profitably, however, after the development of the procarp and the cystocarp had been studied in both genera. It may be noted that structurally the thallus of *Caloglossa* is more complex than that of *Taenioma*.

A question which may here be considered is whether *Taenioma* exhibits a primarily simple or a reduced condition. Since the structure of the thallus, especially that of the indeterminate branches, is comparable to that of many Rhodomelaceae, the most highly evolved Florideae, it may be argued that the thallus of *Taenioma* has been reduced. None the less, the exposed state of the sporangia, coupled with the simplicity of the thallus, favors the view that *Taenioma* actually represents a primitive condition within the Delesseriaceae, that is, a genus which has retained certain relatively simple features characteristic of Ceramiales lower than the Delesseriaceae and other characters which have become elaborated or which have been eliminated in the higher Delesseriaceae.

Within the Delesseriaceae the origin of tetrasporangia from pericentral cells probably is a feature which in itself is indicative of a primitive condition. But it is difficult to evaluate this character in *Taenioma* and related genera, since the thallus is very narrow and the only other cells which conceivably could form sporangia would be the flanking cells. In none of the Delesseriaceae, however, do marginal cells form sporangia. In contrast to *Taenioma*, the sporangia in higher Delesseriaceae are formed by cortical cells and not by pericentral or other primary cells.

In view of the primitive features exhibited by *Taenioma*, it becomes of interest to know whether the genus throws light on the relationships of the Delesseriaceae. Although it is not possible to point to any particular transitional type which could be conceived as forming a link between *Taenioma* and any other family of the Ceramiales, yet certain facts have come to be recognized which have a bearing on the phylogeny of the order and which necessitate a change in the accepted view regarding the relative positions of two of the families, namely, the Delesseriaceae and the Dasyaceae.

In works on the algae, the Dasyaceae are usually placed above the Delesseriaceae. From a review of the literature and the results of the present study it is apparent, however, that the Dasyaceae are phylogenetically lower than the Delesseriaceae. Certain facts furthermore suggest that the Dasyaceae evolved from Ceramiaceae-like ancestors and that the Delesseriaceae and the Rhodomelaceae developed from Dasyaceae-like plants.

It is commonly agreed that the Ceramiaceae include the most primitive Ceramiales. This view is supported by the following facts: (1) The thallus in general is relatively simple, consisting in lower forms of branched monosiphonous filaments but becoming polysiphonous or corticated in higher forms. Typical pericentral cells, that is, cells which from the beginning are as long as the central cells, are, however, not formed. (2) In the majority of forms the sporangia and the gonimoblasts are naked.

(3) The auxiliary cell in lower forms is supplied with a diploid nucleus via an intermediary connecting cell.

Although Kylin (24, 26, 27) has on several occasions expressed the view that the Delesseriaceae and the Rhodomelaceae represent two parallel lines of development, with the Rhodomelaceae occupying a somewhat higher level than the Delesseriaceae, he has, nevertheless, always placed the Dasyaceae above the Delesseriaceae. Phycologists in general have adopted the arrangement of Kylin.

From the work of Rosenberg (38) and others on the Dasyaceae several facts may be cited which indicate that this family is less advanced than the Delesseriaceae and more closely related to the Ceramiaceae than are the Delesseriaceae. The most significant single fact supporting this view is that in the Dasyaceae the auxiliary cell receives a diploid nucleus from the fertilized carposonium via a connecting cell. This feature is characteristic of the lower Ceramiaceae, but has been lost in the Delesseriaceae. Other primitive features of the Dasyaceae are: (1) The sporelings remain monosiphonous for a long time (Killian, 22) as contrasted with those of the Delesseriaceae and Rhodomelaceae in which pericentral cells are formed at an early stage in development. (2) The pericentral cells are of a rudimentary character in certain genera. (3) The sporangia remain partially exposed.

It may also be added that Falkenberg (14) considered the sympodial method of branching of the Dasyaceae as a character which is primitive in comparison with the monopodial branching characteristic of the Rhodomelaceae. Whether the sympodial habit actually is a primitive feature or whether it is a derived condition which has become established in the Dasyaceae would, however, be difficult to decide. It would seem that in exogenous branching a reversal from the monopodial to the sympodial habit or vice versa is one which would not entail profound change. Furthermore, in the Ceramiaceae, which are more primitive than the Dasyaceae, some forms show monopodial and others sympodial branching (Feldmann-Mazoyer, 16, p. 123).

According to Kylin (28, p. 134) the sporelings of the Dasyaceae show monopodial branching. If this were correct it would indicate that the sympodial habit of the older thallus was acquired in the course of evolution of the family. However, from the observations of Killian (22) on the sporelings of *Dasya arbuscula*, upon which work Kylin's statement is based, it seems evident that sympodial branching is also characteristic of the sporelings of the Dasyaceae, or at least of those of *D. arbuscula*. This is the interpretation which Oltmanns (34, p. 322) also gives of Killian's work.

As to the relative position of the Delesseriaceae and the Rhodomelaceae the available facts favor the conclusions of Kylin (24, 26, 27) that these families represent two parallel lines of

evolution, with the Rhodomelaceae occupying a somewhat higher level than the Delesseriaceae. In support of this view Kylin (26, 27) cites three facts: (1) The Rhodomelaceae are in a more active state of speciation. (2) In the Rhodomelaceae the pericarp is initiated prior to fertilization whereas in the Delesseriaceae it is formed after fertilization. (3) In the Rhodomelaceae, the cover cell of the procarp is a specialized cell which degenerates if fertilization fails to occur while in the Delesseriaceae it is comparable to an ordinary vegetative cell (Kylin, 24, p. 102; 28, p. 286).

It may be pointed out, however, that the two latter distinctions only hold when the Rhodomelaceae are contrasted with the Delesseriaceae. In the higher Delesseriaceae, that is, in the Nitophylleae, the cover cell of a procarp behaves like that of the Rhodomelaceae (Kylin, 28, p. 286); and in certain members of this sub-family (e.g., *Phycodrys sinuosa* Kylin, 24, figs. 46h, 47d-g; *Acrosorium acrospermum* Papenfuss, 36, fig. 16) the pericarp is initiated prior to fertilization.

To the points cited by Kylin may now be added a fourth which lends support to the view that the Rhodomelaceae are phylogenetically higher than the Delesseriaceae. In the Rhodomelaceae the sporangial mother-cells cut off the cover cells before the sporangia are initiated whereas in the Delesseriaceae the cover cells are formed after a sporangium has been initiated. In the latter group the young sporangia are thus exposed while in the Rhodomelaceae they are protected. In *Taenioma*, the most primitive of known Delesseriaceae, the cover cells are rudimentary and serve no protective purpose at any stage in the development of the sporangia, while in the related *Platysiphonia* the cover cells are well developed on one surface of the fertile branches and rudimentary on the other. Thus *Platysiphonia* may be said to form a link between *Taenioma* and *Vanvoorstia* in which latter genus the cover cells are well developed on both surfaces of the fertile blades (Papenfuss, 35).

As to the probable ancestors of the Delesseriaceae, there is reason to believe that they may have evolved as an off-shoot from the stock which gave rise to present-day Dasyaceae. Three facts especially may be cited in support of this view: (1) In the Delesseriaceae as in the Dasyaceae the sporangial mother-cells first form a sporangium and then the cover cells. (2) In both the Delesseriaceae and the Dasyaceae the cover cell of the procarp is comparable to a vegetative cell and functions as such if fertilization fails to occur. (3) In the Delesseriaceae in general, but more particularly in the Delesseriaceae, as well as in the Dasyaceae the pericarp is not initiated until after fertilization.

It is of interest to note that in these three features the Rhodomelaceae have advanced beyond both the Dasyaceae and the Delesseriaceae. It may be mentioned, however, that the higher

Delesseriaceae, for example, certain members of the Nitophylleae, not only share some of these advances with the Rhodomelaceae but have attained a degree of simplicity which surpasses that shown by any of the Rhodomelaceae. It is thus found that: (1) In the Nitophylleae growth of the mature thallus is usually marginal whereas in the Rhodomelaceae it is primarily apical. (2) In the Nitophylleae intercalary cell divisions are of common occurrence while such divisions, to the writer's knowledge, are unknown in the Rhodomelaceae. (3) In the Nitophylleae the reproductive organs are formed in parts away from the central axis of the thallus whereas in the Rhodomelaceae they generally are localized on the axis, that is, the pericentral cells. It is of interest to note that an advance in the same direction is shown by some of the higher Rhodomelaceae, such as *Laurencia* and *Ricardia*. In these genera the sporangia are no longer formed by pericentral cells but by cells farther away from the central cells (cf. Kylin, 26, p. 101).

Finally, in regard to the probable prototypes of the Rhodomelaceae, it seems likely that this family also may have evolved from Dasyaceae-like algae, although at a time subsequent to the separation of the Delesseriaceae. It is well known that the Rhodomelaceae have a number of characters in common with the Dasyaceae. The similarity in the habit of the thalli, the formation of the sporangia from pericentral cells, and the corresponding position of the spermatangia are some of the more important points of agreement which may be mentioned. It is of interest to note in this connection that in *Heterosiphonia coccinea* (Dasyaceae) the pericentral cells are formed in the manner characteristic of the Rhodomelaceae except in the fertile segments of female plants where they are formed in typical dasyacean fashion (Rosenberg, 38). In this particular species the sporangia and their cover cells are also formed in the sequence characteristic of the Rhodomelaceae. This member of the Dasyaceae thus shows certain morphological features which have become established in present-day Rhodomelaceae. It may further be mentioned that Falkenberg (14) considered the Dasyaceae, as now recognized, as a sub-family in the Rhodomelaceae and regarded them as the ancestors of all other Rhodomelaceae.

A schematic representation of the probable interrelationships and lines of development of the families of the Ceramiales is given in text figure 1.

SUMMARY

The results of this study show that *Taenioma* does not belong to the Rhodomelaceae, in which it has been placed by certain writers, but to the Delesseriaceae. This is shown by the plan of pericentral cell formation, the manner of division of the lateral

pericentral cells, and the method by which the sporangia are formed.

From the simple structure of the thallus and the exposed condition of the sporangia, it is concluded moreover that *Taenioma* is the simplest of known genera of the Delesseriaceae.

The branches of *Taenioma* are exogenous in origin. Although characteristic of the other families of the Ceramiales, this method of branching is rarely encountered in the Delesseriaceae and in addition to *Taenioma* is known to occur in *Caloglossa* only.

The sporangia are initiated by the lateral pericentral cells and are formed before the mother-cells have cut off cover cells. The latter feature is recognized as one whereby the Delesseriaceae

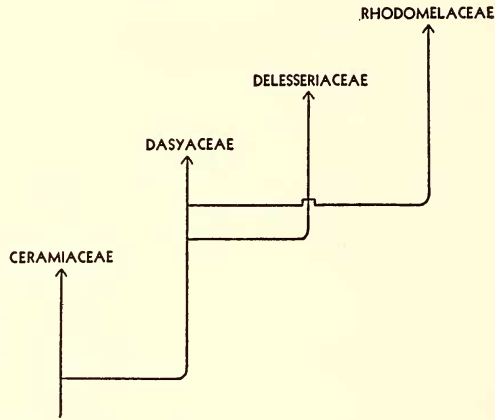


FIG. 1. Diagrammatic representation of the probable interrelationships of the families of the Ceramiales.

may be distinguished from the Rhodomelaceae. In the Rhodomelaceae the mother-cells first form cover cells and then a sporangium.

Taenioma perpusillum and *T. macrourum* are considered as separate species. The primary distinguishing feature lies in the fact that the determinate branches of the former form three and those of the latter two terminal hairs. These hairs are initiated in a precise manner by the apical cell and do not vary in number.

Taenioma Clevelandii, the only other species which has been credited to *Taenioma*, is transferred to the genus *Platysiphonia* with which it is shown to share various morphological features.

The phylogeny of the Ceramiales is discussed. Evidence is produced to show that the Delesseriaceae are more highly evolved than the Dasyaceae. Additional evidence is furnished in support of the view of Kylin that the Rhodomelaceae are the most highly evolved Ceramiales. It is concluded that the Dasyaceae evolved

from Ceramiaceae-like and the Delesseriaceae and Rhodomelaceae from Dasyaceae-like ancestors.

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After the study had been completed, it was learned from Dr. C. K. Tseng that he had also been working on *Taenioma*, and had arrived at the same conclusions as the writer with respect to the systematic position of the genus and the taxonomy of the species.

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